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The Classic

Origin and Comparative Anatomy of the Pectoral Limb

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Origin of Paired Appendages

The origin of paired appendages has been the source of considerable controversy among morphologists. The lateral-fin theory has supplanted the gill-arch theory of Gegenbaur and is now accepted as the most plausible explanation of the beginning of these appendages.

According to the lateral-fin theory, paired limbs are derived from longitudinal lateral folds of epidermis extending backward along the body from just behind the gills to the anus. By accentuation of the anterior and the posterior and suppression and reduction of the intermediate portions of the folds the pectoral and the pelvic fins were formed (Fig. 1). Into these folds muscle buds migrated from the ventral border of the adjoining myotomes, giving rise to radial muscles which motivated the fins and were the forerunners of the intrinsic muscles of the hand (Bunnell). The muscle buds disclosed a metameric arrangement and derived their nerve supply from ventral roots of the spinal nerves.

Peripheral nerve fibers in the base of the fin divide repeatedly, giving rise to a complex plexus. The number of myotomes which comprise the muscular apparatus of the

fin is disclosed by the number of spinal nerves which contribute to the plexus. In ontogeny, motor nerves always supply the muscles for which they were designed originally. Muscles exhibiting a nerve supply from more than one spinal nerve denote combining of muscular tissue of several segments. Next in the process of evolution of the appendages was the appearance of radials (cartilage rays) between the muscles buds; these provided more strength and support to the fins (Fig. 2).

Concentration and fusion of the proximal (basal) ends of the radials in the fin gave rise to the basilia (basal cartilages) which extended inward into the body wall to form the most primitive girdle (Fig. 3). In order to meet the requirements of a freely movable fin an articulation appeared in the basal plates. Further evolution of the girdle includes fusion of the basilia of either side in the midline to form a ventral bar; also included is a dorsal extension of the arch above the level of the articulation to join the axial skeleton. Thus a complete girdle is formed around the body. The above steps in the ontogeny of the girdle have been noted in the *Selachia* (elasmobranches) and also in *Chondrostei* and *Teleostei*.

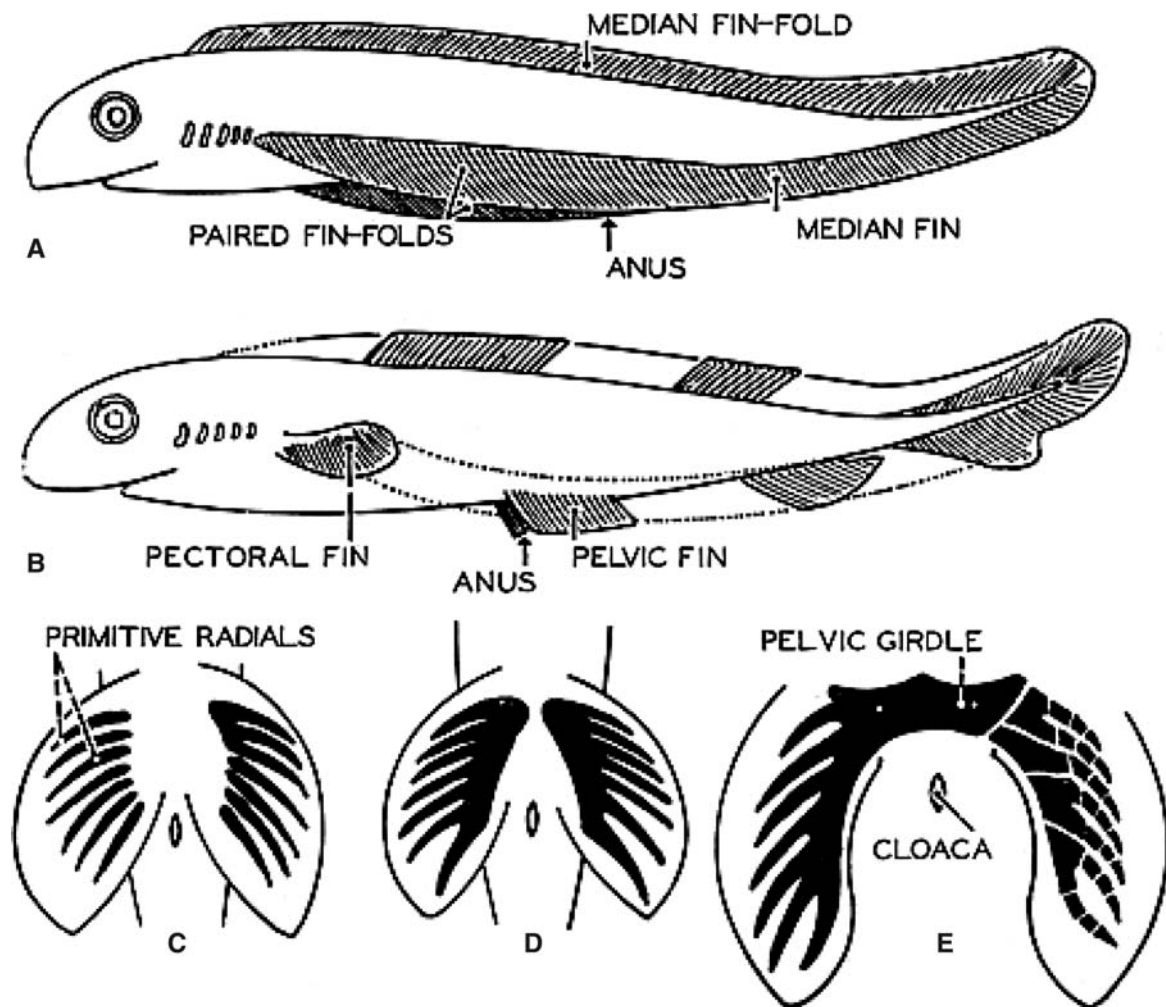


Fig. 1A–E Hypothetical evolution of paired fins and their skeletal supports. (A) Primitive stage, characterized by continuous fin folds; the dorsal and ventral fins posterior to the anus are median and unpaired. (B) Elasmobranch stage; paired fin-folds persist only in the region of the pectoral and pelvic fins; median fins have become discontinuous. (C–E) Hypothetical stages in the evolution of the

skeleton of the pelvic fins of elasmobranch fishes. The right side of C and E represents a later stage in the phylogenesis than the left. E represent the differentiated skeletons of the girdle and the extremity (after Wiedersheim). (Neal and Rand: Chordate Anatomy, Philadelphia, Blakiston)

Evolution of the Pectoral Girdle

Fishes

In its basic pattern the girdle is an inverted arch spanning the ventral surface of the body and extending dorsally on either side above the level of the articulation. Both the girdle and the limb are free. Each girdle comprises a ventral segment (coracoid) and a dorsal segment (Scapula). These at the point of juncture form the glenoid fossa, which articulates with the basal component of the skeleton of the limb. Further segmentation of the scapula gives rise to the suprascapula, which may become attached to the axial skeleton (as in skates). All the above elements have separate centers of chondrification (Fig. 4).

Further in the scale of evolution of the pectoral girdle is the appearance of a girdle of membranous bones derived from the skin. It encircles the head starting from behind the gills. The elements of either half of the girdle join and fuse in the midline on the ventral surface of the body through the medium of the interclavicle. Each half of this membranous circle consists of four membranous bones: (1) post-temporal, which is jointed with the skull, (2) supra-cleithrum, (3) cleithrum and (4) clavicle.

The interclavicle which unites the girdle ventrally is an unpaired bone. Both the basal girdle and membranous girdle eventually became attached to one another. Such is the basic plan of the pectoral girdle as noted in two genera (*Eusthenopteron* and *Sauripterus*) of the upper Devonian crossopterygians. These are considered the ancestors of the

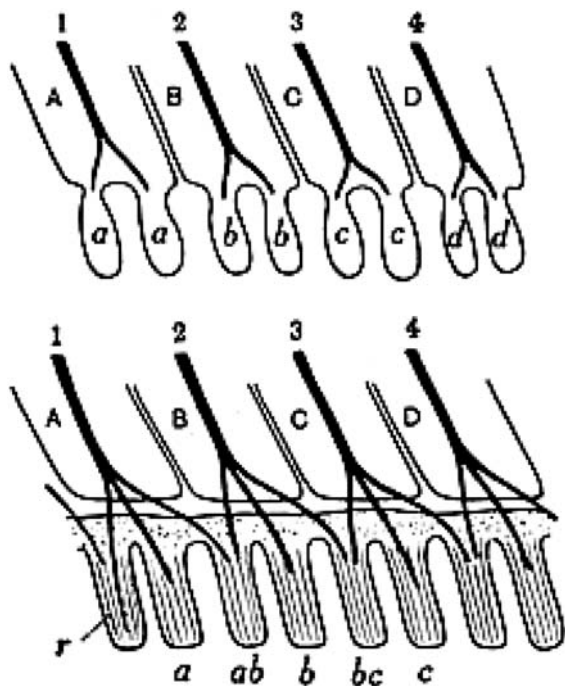


Fig. 2 Formation of adult radial muscles from embryonic muscle buds, and their motor nerve supply. Above, embryonic stage with a pair of buds to each segment; below, adult stage with radial muscles compounded of material from adjacent buds, 1–4, four spinal nerves; A–D, four myomeres; a–d, muscle buds; r, radial muscle. (Goodrich, E. S.: *Studies on the Structure and Development of Vertebrates*, London, Macmillan, p. 134)

amphibia whose appendages possessed the pattern which made the evolution of the tetrapod limb possible (Fig. 5).

Amphibia

With the attainment of terrestrial habits most of the elements of the membranous girdle (post-temporal and supracleithrum) decreased in size and disappeared, while the cartilaginous girdle began to assume a more significant role. The skull was freed of all attachment to the girdle. In urodels all vestiges of the membranous girdle have disappeared.

In the amphibia the tripartite type of pectoral girdle made its first appearance; the coracoid represented by the ventral bar in the fishes became segmented into the anterior procoracoid and posterior coracoid, while the clavicle came in relation to the procoracoid. No significant alterations occur in the suprascapula and the scapula. A noteworthy observation in the pectoral girdle of large amphibia (*Rhachitomi*) is the direction of the glenoid fossa. It faces laterally, indicating that the humerus extended away from the trunk in the ground. Its articular surface was “screw-shaped” (Howell), indicative of clumsy arm movement.

Reptiles

Whereas in the amphibia the pectoral girdle is just behind the head, in the reptile it has migrated a considerable distance from this position. Essentially, the girdle comprises a scapula, a procoracoid and a coracoid. In general, the clavicle replaces the procoracoid, as evidenced by the latter’s reduction in size. However, in some reptiles the clavicle is absent (*Crocodylia* and *Chamaeleo*). Some reptiles lost their limbs, and the girdles are either greatly reduced or have disappeared (*Amphisbaenienes*, *Ophidia*).

Birds

Elements of the girdle of the reptiles were modified in birds to permit flight. The clavicles exhibit a marked degree of development, their ventral ends fusing to form the wish-bone (furcula). The scapula is small, curved and narrow, extending backward. The coracoid is large and strong, one end together with the scapula forming the glenoid fossa, while the other unites with the sternum. The keeled sternum provides attachment for the strong pectoral muscles used in flight. In some cursorial birds the clavicles are greatly (emu), while in others they are absent.

Mammals

In monotremes, the lowest order of mammals, large coracoids are found between the sternum and the glenoid fossa. In all other mammals, however, the coracoid tends to become greatly reduced, forming an insignificant process on the scapula. The only other vestige of the bone, is the coracoid ligament, extending from the coracoid process to the bone, in which may be found isolated masses of cartilage. It has a separate center of ossification. This arrangement frees the scapula from any bone attachment to the skeleton. In mammals without clavicles the scapula has no bony attachments whatsoever. It becomes the sole support for limb and provides attachments for muscles necessary for a freely movable extremity. New functional demands on the girdle resulted in the development of a projection of bone on the dorsal surface of the scapula (spina scapulae) which extends downward and ends in the acromion.

Generally, the clavicle articulates with the acromion and the sternum, its only connection to the coracoid process being by the coracoclavicular ligaments (conoid, trapezoid). In mammals which have acquired freedom of the forelimb to a marked degree, such as insectivores, primates and some marsupials and rodents, the clavicle is usually well developed. In others, including ungulates, carnivores, cetaceans and some rodents, edentates and marsupials it is absent or rudimentary.

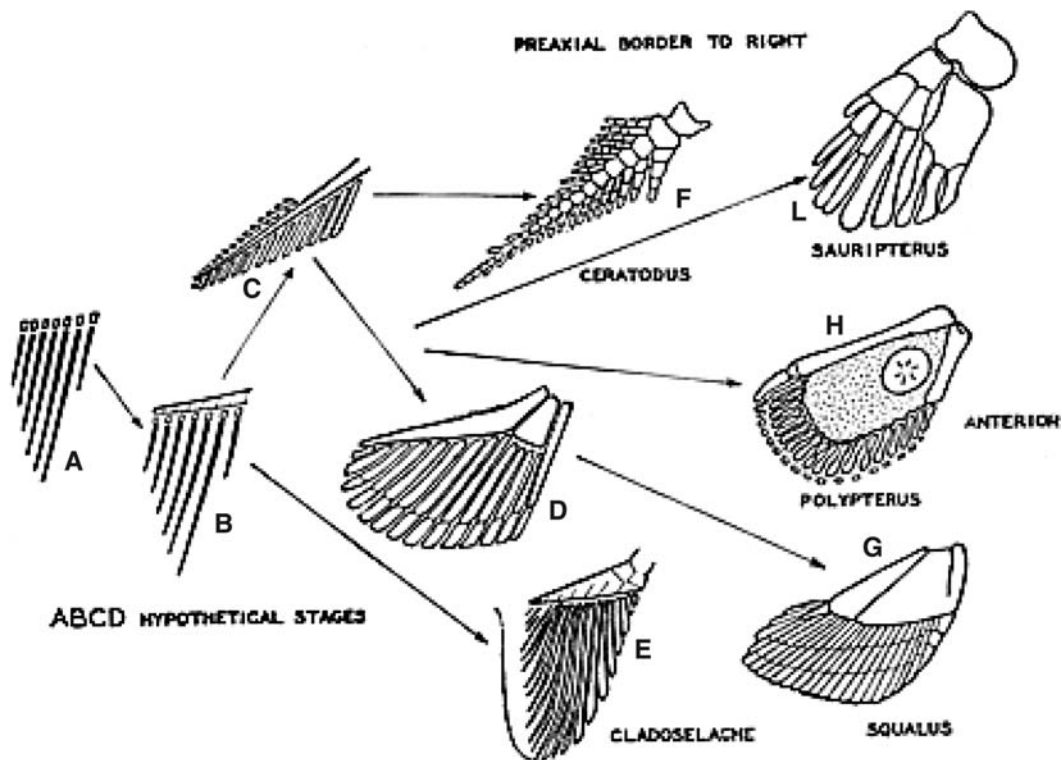


Fig. 3 Diagrams illustrating hypothetical evolution of the extremities of diapnoan (I), ganoid (H) and elasmobranch (G) from a fin fold supported by a series of similar radial cartilages. By fusion of radial cartilages basilia (basal cartilages) are formed. Skeletal supports of

the fins eventually differ in relation of the basal elements to the radialis (Redrawn from A. Brazier Howell). (Neal and Rand: Chordate Anatomy, Philadelphia, Blakiston)

Evolution of the Upper Extremities

There has been considerable controversy as to the derivation of the cheiropterygium (tetrapod limb, also called the pentadactyl limb) from the ichthyopterygium (paired fins of fishes). It was recorded previously that in the evolution of the free paired appendages the proximal or basal ends of the radials (cartilage rays) fused to form basilia, and later with the demand of greater movability of the fin a joint appeared between the radials and the basilia, several of which in turn articulated with the girdle. Such a scheme is discernible in the paired fins of the elasmobranchs, which possess three basilia (propterygium, mesopterygium and metapterygium) located between the girdle and the radials of the fin (Fig. 4).

In the pectoral girdles and the fins of the crossbouts, *Eusthenopteron* and *Sauripterus* (fossils from upper Devonian), is found an arrangement of the skeletal elements, generally accepted as a link between paired fins of fishes and tetrapod limb (Fig. 5). These two genera of crossbouts are considered close to the forms from which the amphibia evolved. The basic pattern of their pectoral limb comprised a proximal segment, which

in turn articulated with several distal elements. The proximal element was destined to become the humerus, the middle elements the radius and the ulna, the distal elements the carpus and the digits.

The change from an aqueous to a terrestrial existence was accompanied by pronounced alteration in the skeletal elements of the pectoral fin which now must be used for support and locomotion. Therefore, in the amphibia, the first animals to adopt terrestrial habits, the pentadactyl limb evolved from the paired fins. From the distal element arose the carpus, the metacarpus and the phalanges. The principal element in the radial side became the thumb, and those on the ulnar side the other four digits. In all stages of evolution up to and including man the basic plan of the pentadactyl limb was maintained.

Scapula

During the evolution of the upper extremity, the scapula, more than any other bone of the shoulder girdle, reflects momentous alterations that have been brought about by increased functional demands of a prehensile limb. Changes in posture provided the stimulus which initiated the

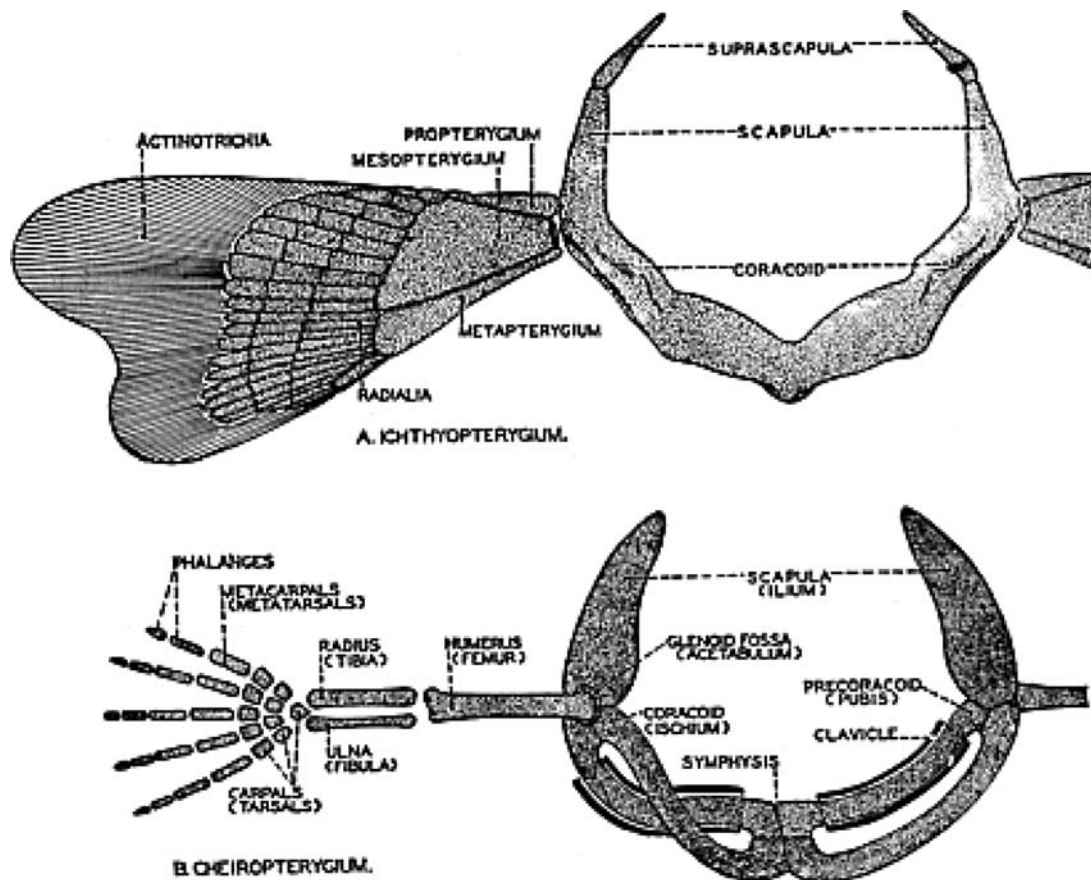
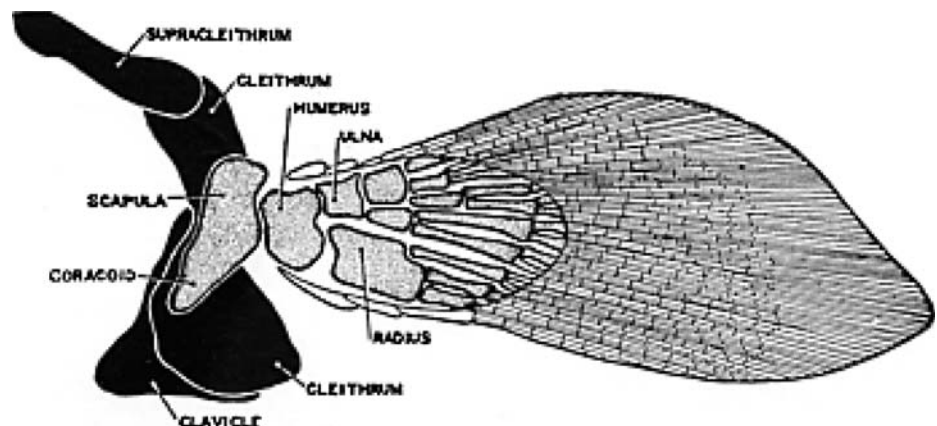


Fig. 4 Diagrams illustrating scheme of pectoral appendages of lower and higher vertebrates. (*Bottom*) Names of corresponding parts of pelvic appendages are shown in parentheses. (Neal and Rand: Chordate Anatomy, Philadelphia, Blakiston)

Fig. 5 Diagram of reconstructed pectoral girdle and fin of *Sauripterus* and upper Devonian crossopterygian fish. It exhibits a close similarity of relations of proximal elements of extremity to those found in the pectoral extremity of tetrapods (redrawn from Brown). (Neal and Rand: Chordate Anatomy, Philadelphia, Blakiston)



numerous morphologic changes. In the cervical region but was freed from the skull. Rhachitinous amphibians possessed massive scapulae with the glenoid cavity pointing laterally. The articulating surface was screw-shaped, and the limbs were held in the coronal plane horizontal to the ground.

In the Reptilia the scapula with the entire girdle migrated a great distance from the skull in order to permit a more efficient mode of locomotion. The scapula was still broad and massive in the primitive forms. However, later with increased efficiency in locomotion, there was a trend toward reduction of this bone, the glenoid cavity shifting

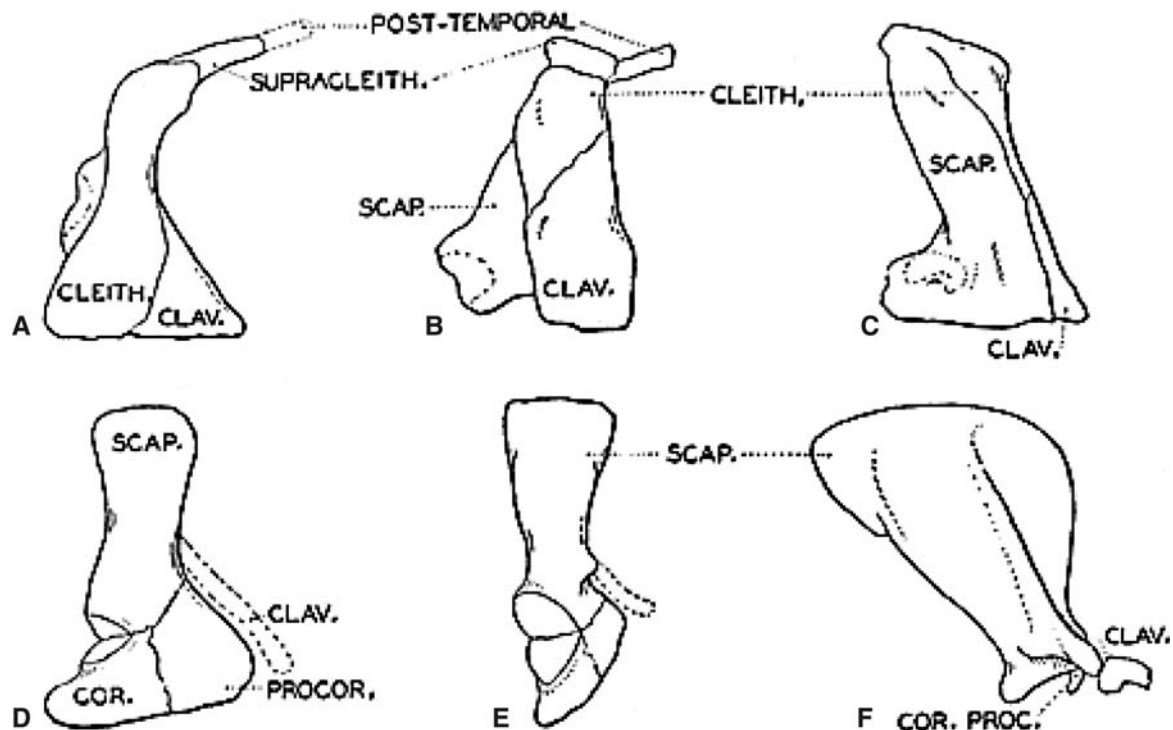


Fig. 6A–F Phylogenesis of the pectoral girdle. (A) Sauripterus (Devonian crossoterygian lung fish). (B) Eogyrinus (Carboniferous embolomorous amphibian). (C) Eryops (Permian rhachitomous amphibian). (D) Moschops (Permian dinocephalian reptile). (E)

Cynognathus (Triassic theriodont reptile). (F) Macaca (an Old-World Recent monkey). (Howell: Speed in Animals, University of Chicago Press, p. 138)

from a position directed laterally to one directed posteriorly and inferiorly. As a result of the change in posture, the coracoid's function decreased. Hence, a gradual reduction in its size is noted in this group. Up to this stage in evolution of the pectoral girdle no evidence of a spine on the dorsal surface of the scapula is found except in the Therapsida whose posture is not unlike that of the mammals.

Posture was responsible for the development of the scapular spine which is found in all mammals except the very primitive forms, the Monotremata. With rearrangement of some and disappearance of other muscles, the need of a procoracoid and coracoid no longer existed. Therefore, the former element disappeared entirely, while the latter was reduced to the coracoid process. The shape of the scapula is dependent upon posture and the functional requirements of the muscles attached to it. It is broad and massive in forms which need large powerful serratus anticus muscles to support heavy bodies in a quadruped position.

In mammals which have partially or completely freed the pectoral limbs, the shape of the scapula exhibits a trend towards the pattern found in man. These alterations are brought about by change in posture from the pronograde to the orthograde and highly specialized functional requirements of a prehensile limb. The most significant scapular change is in the relation of length to breadth of a bone.

Pronograde forms disclose a long narrow scapula, while in the ascent toward man it becomes broader.

This morphologic change is most obvious in the primates. That portion of scapula below the spine demonstrates the most pronounced alterations, those in the region above the spine being insignificant. Morphologic modifications in the scapula can be expressed by a scapular index, a ratio of the breadth (measured along the base of the spine) to the length (measured from the superior from the inferior angle). The scapular index is high in the pronograde in which the scapula is long, narrow and slender. The index progressively decreases in the successive stages of development approaching man (orthograde).

This is the result of a gradual increase in the breadth of the scapula and elongation of the bone below the level of the spine, giving rise to a progressive increase in the "infraspinous index" (Fig. 7). Inman, Saunders and Abbott, in their comprehensive study of the function of the shoulder joint, observed that lengthening of the scapula below the spine changed the relation of the axillary border of the scapula to the glenoid fossa, thereby altering the angle of pull of the muscles attached to this region, a feature of great significance in the mechanism of the shoulder.

In the primates, as one approaches man, the increasing importance of the role of the deltoid muscle as reflected in

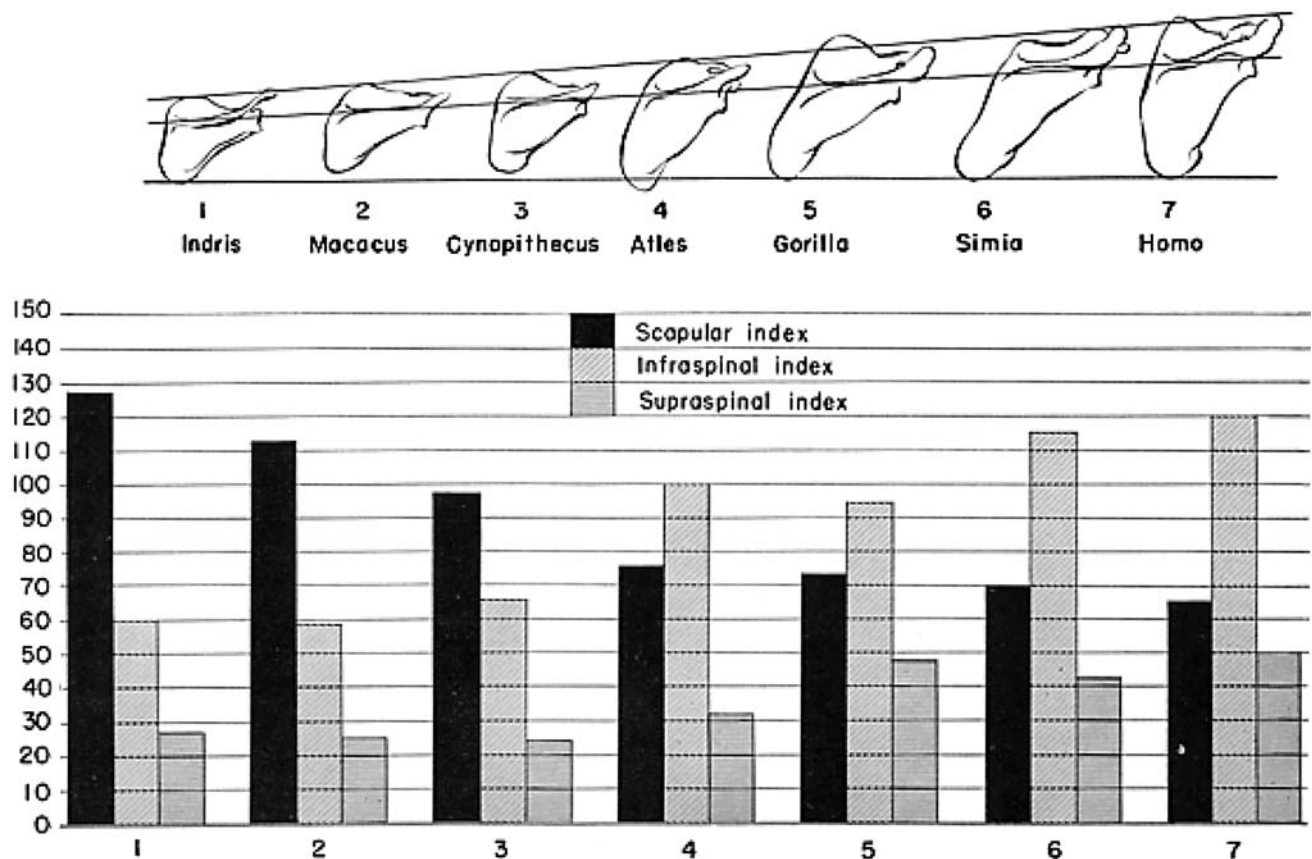


Fig. 7 Progressive decrease in scapular index in successive stages from the pronograde to the orthograde. (Redrawn from Inman, Saunders and Abbott: *J. Bone & Joint Surg*, 26:2)

the prominence of the outer end of the spine, the acromion process. Whereas in pronograde forms the acromion process is insignificant, in orthogrades it is a massive structure overlying the humeral head (Fig. 8).

Humerus

During evolution of a prehensile extremity, profound morphologic modifications occurred in the humerus. In rhachitinous amphibians the humerus was a massive bone flattened at either end, the distal end being larger than the proximal to provide attachment for large forearm muscles. In reptiles with free motion in the forelimb the upper extremity was brought beneath the body, and the humerus became less massive. Two nodules appeared at the proximal end, which evolved into the tuberosities of the mammalian humerus. The anterior became the greater, and the posterior the lesser tuberosity.

Generally speaking, in mammals adapted for running (ungulates—horse) the articular surface of both ends of the humerus function in the same plane (sagittal plane), a line passing through the long axis of the head of the humerus, is

directed forward and one through the distal articular surface transversely. Meeting of these two axes describes a torsion angle of 90°. In primates, as the orthograde form is approached, the torsion angle increases. Man discloses some variation in the torsion angle; Australians exhibit an angle of 134°, and the French and the Swiss 164° (MARTIN, 1928).

Several factors are responsible for the changing relationship of the articular surfaces of the humerus. Development of the orthograde forms was accompanied by antero-posterior flattening of the thoracic cage and dorsal displacement of the scapula. The glenoid fossa is now directed laterally (Fig. 9). Prehensile requirements, however, demand that the extremity as a whole function anterior to the body and that the elbow be maintained in the parasagittal plane. To meet these specifications, the humeral shaft twists inwardly, while the articular surfaces at either end rotate in the opposite directions (Fig. 10). The dominant role acquired by the deltoid in the higher primates is demonstrated further by the progressive shift of the deltoid insertion on the humerus to more distal position. This feature, together with increase in size of the acromion,

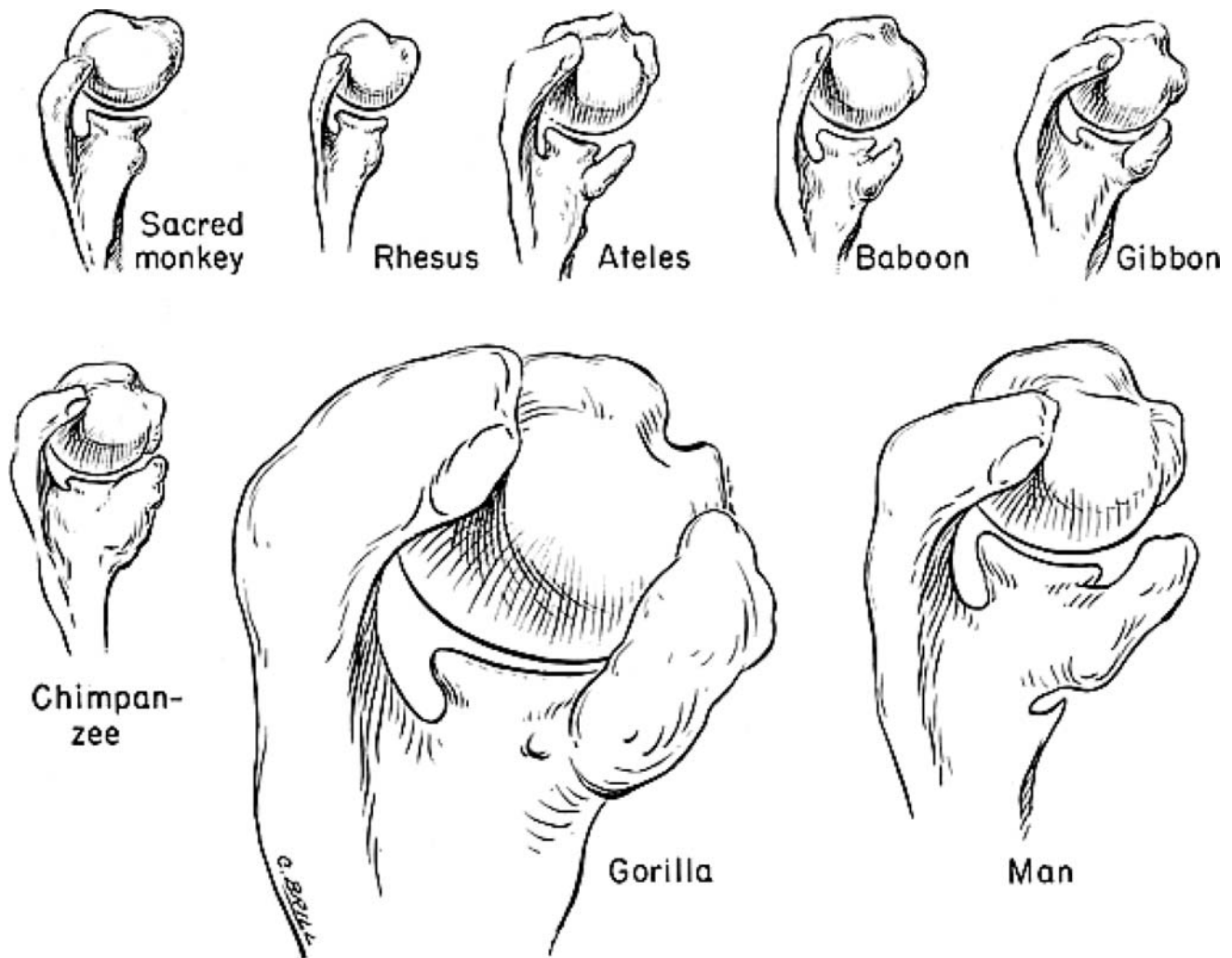


Fig. 8 Gradual increase in spine of the scapula and the acromion process during development from the pronograde to the orthograde. This change reflects the increasing importance of the deltoid muscle. Also

note the increase in size of the coracoid process, the inequality of the two tuberosities of the head of the humerus and the inner displacement of the intertubercular sulcus in successive stages of development.

greatly increases the leverage of the deltoid muscles (Fig. 11).

Other significant morphologic alterations were recession of the lesser tuberosity and medial displacement of the bicipital groove. Pronograde forms disclose the biceps tendon passing over the center of the head of the humerus and entering the groove in the same plane. In this position it acts as a strong elevator of the arm. Both tuberosities in these forms are approximately the same size.

A different relationship is found in orthogrades. In these forms, the bicipital groove has been rotated medially by torsion of the humerus so that a line passing through the center of the head of the humerus in man makes an angle of 30° with one passing through the plane of the groove (Inman, Saunders and Abbott). Marked reduction in the size of the lesser tuberosity is a characteristic feature in the higher primates.

From the above observations it is obvious that the biceps tendon (long head) functions at a greater mechanical disadvantage, further increased by using the arm in a position of internal rotation. In this position the biceps tendon plays over the medial wall of the groove, and the lesser tuberosity now really functions as a trochlea.

Muscles

Changes in posture and functional requirements of a prehensile extremity were responsible for alterations in the topography and the morphology of muscles about the shoulder. Such changes were primarily responsible for the skeletal modifications previously indicated. The extent of the change in any individual muscle becomes apparent when its relative mass is compared with the total mass of the group in which it belongs. Following the scheme of

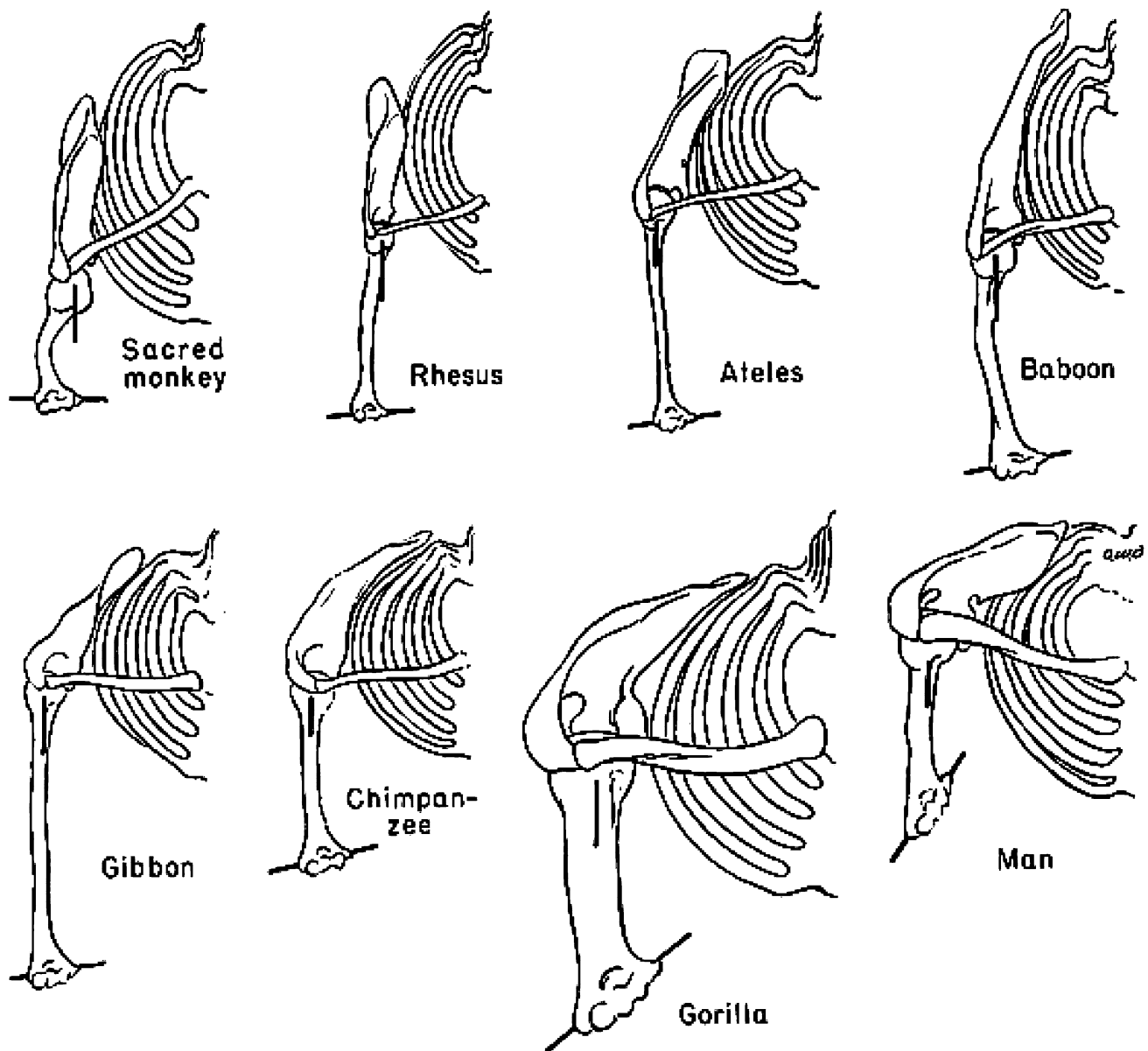


Fig. 9 Changes in the thoracic cage, the scapula and the humerus, in successive stages from the pronograde to the orthograde. The thoracic cage shows flattening in the antero-posterior plane, and the scapula

migrates to a dorsal position so that the glenoid cavity is directed laterally. The humerus shows a progressive increase in the torsion angle.

Inman, Saunders and Abbott, the muscles which partake in shoulder mechanism can be categorized into three topographic units: (1) Scapulohumeral group, (2) axiohumeral group and (3) axioscapular group.

The study made on the functional mechanism of the shoulder by the aforementioned workers is so complete, comprehensive and logical that one is forced to draw heavily from this source of information when discussing this topic. Many of their observations are noted in the subsequent section.

The Scapulohumeral Group. These connect the scapula to the humerus and consist of the supraspinatus,

infraspinatus, teres minor, subscapularis and deltoid muscles. Concurrently with acquisition of a free limb, the relative deltoid mass increases, while that of the supraspinatus decreases. Forty-one per cent of the total mass of this unit in man is made up by the deltoid muscle.

Comparative anatomy further discloses that the teres minor muscle is wanting in early mammals and that it evolved from the deltoid to form a separate muscle passing from the inferior angle of the scapula to the humerus. With elongation of the infraspinatus portion of the scapula, the relative mass of this muscle progressively increased until, in man, it makes up 5 per cent of the total mass. Although

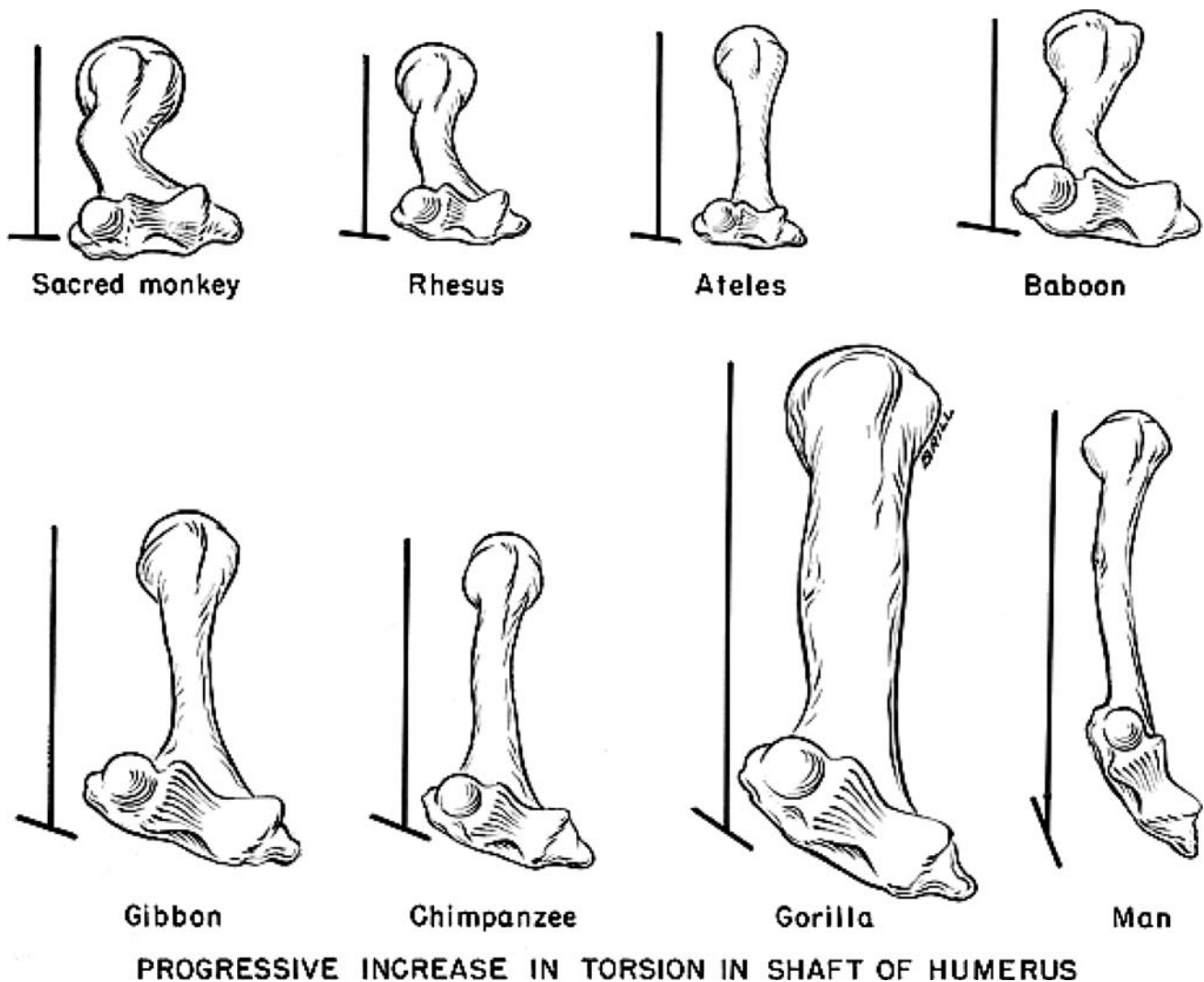


Fig. 10 Progressive increase in torsion of the humerus resulting in inward rotation of the bicipital groove. The articular surfaces at either end of the humerus rotate in opposite directions.

it is a morphologic component of the deltoid, teres minor, because of topographic changes, plays an entirely different role in the mechanism of the shoulder than of the deltoid.

The subscapularis muscle is little affected by morphologic alterations from the primitive to the higher primates. It makes up 20 per cent of the mass of the scapulohumeral group. The only significant alteration is an increase in number of fasciculi of origin. This is the result of elongation of the scapula. This same skeletal change brought about an increase in the area of attachment of the infraspinatus, which constitutes approximately 16 per cent of the total mass.

According to Inman, Saunders and Abbott, the last three muscles (subscapularis, teres minor and infraspinatus), by reason of alterations in the morphology and the topography of the group and the elongation of the scapula, function as a

unit. They are both rotators and depressors of the head of the humerus.

The axioscapular group, chiefly concerned with the mechanism of the shoulder, comprises (1) serratus anterior, (2) rhomboids, (3) levator scapulae and (4) trapezius muscles. The first three muscles of this unit originated from the ribs (first eight or ten) and their homologues (transverse processes of the cervical vertebrae) in the cervical region and inserting into the vertebral border of the scapula. In primitive forms the dominant function of this group was to control the movements of the vertebral border of the scapula.

In general, those fibers concerned with dorsal motion of the scapula became the rhomboid muscles; those with ventral motion, the serratus muscle; and those with cranial displacement of the scapula, the levator scapulae. Function

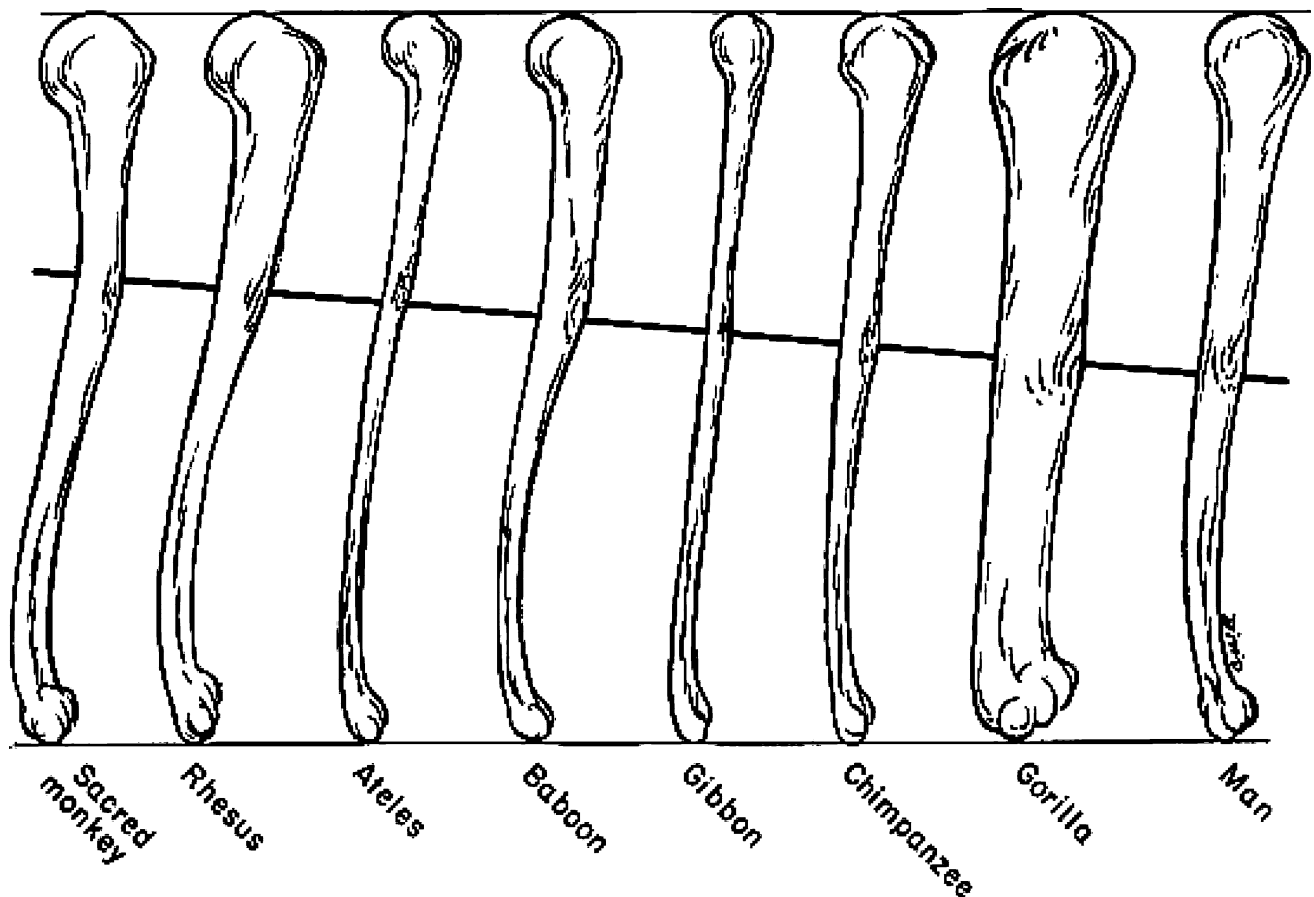


Fig. 11 Deltoid insertion migrates progressively to a lower level on the shaft of the humerus, indicating the significant role played by the deltoid in higher primates.

and posture were responsible for evolution of the individual muscles as they exist in the higher primates. The serratus anterior formed the basal unit for all three muscles. Concentration of the proximal and distal fibers and progressive reduction of the intermediate fibers gave origin to two distinct muscles, the levator scapulae and serratus anterior.

Further morphologic alterations in the serratus anterior comprise grouping of its proximal and distal fibers, progressive reduction in size of its intermediate fibers, and insertion of the dominant upper and lower portions of the muscle into the superomedial and inferior angles of the scapula.

The trapezius, like the sternocleidomastoid muscle, evolved from a muscle sheet passing from the last gill arch to the membranous girdle. In terrestrial forms it attained a position from the occipital region to the trunk; in tetrapods it arises from the occiput, the middorsum of neck and thorax, and inserts into the spine of the scapula, the acromion and the scapula. Little change has occurred in the trapezius in the evolution of the primates. There has been,

however, some concentration of its proximal and distal muscle components and reduction in mass and efficiency of its middle components.

The axiohumeral group is made up of the pectoralis major, the pectoralis minor and the latissimus dorsi muscles and extends from the trunk to the humerus. The pectoral group evolved from a primitive muscle sheet which connected the coracoid with the humerus. Change in posture and increased functional demands made on the limb were responsible in the later reptilian and early mammalian forms for displacement of part of this muscle sheet dorsally to gain attachment to the scapula which later gave rise to the supraspinatus, the infraspinatus and the interior part of the subscapularis. All other components of the muscle migrated from the procoracoid to the sternum and gave rise to the pectoralis major.

Further morphologic modification in the pectoralis major resulted in a division of this mass into a superficial and a deep layer. Part of the sternal attachment of the superficial fibers shifted forward and gained attachment to the clavicle (clavicular head of the pectoralis major). From

the deep layer evolved the pectoralis minor muscle which, in higher primates, discloses its humeral attachment in primitive forms to have migrated to the coracoid process.

The latissimus dorsi and teres major muscles originate from a single basic muscles sheet extending from the trunk, caudal to the scapula, to the humerus. They demonstrate in the higher primates no significant morphologic or topographic alterations except that they are unusually well developed in forms specializing in climbing.

Biceps Brachii and Triceps Muscles. Both these muscles evolved from ventral and dorsal brachial muscle elements which were concerned primarily with motion in the more distal joints, the elbow and the wrist. From the ventral brachial elements arose the biceps muscle by proximal migration along a fascial plane of brachial components to reach the scapula (Howell). In mammals other than primates, it is a single muscle. Cursorial forms (horse) disclose powerful biceps which together with the supraspinatus act as a single functional unit to elevate the foreleg.

Primates exhibit two heads of origin: one from the supraglenoid tubercle and the other from the coracoid process. Medial displacement of the bicipital groove resulting from torsion of the humeral shaft places the long head at a mechanical disadvantage, thereby losing its efficiency as an elevator of the arm which it possesses in other forms. However, the biceps can be made to function as an abductor of the extremity if the arm is rotated externally; hence, restoring the tendon to the top and the center of the humeral head. This maneuver is not infrequently utilized by individuals with paralyzed abductors of the arm.

The triceps originated from a dorsal brachial muscle element. Like the biceps, its three heads migrated proximally. The scapular or long head gained attachment on the infraglenoid tubercle, the medial head to the upper and posteromedial surface of the humerus, and the lateral head

to the upper and posteromedial surface of the humerus, and the lateral head to the upper posterolateral surface. No significant morphologic or topographic alterations have occurred in this muscle. It functions as a powerful extensor (dorsal flexor) of the arm.

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